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ON THE PHYLOGENETIC RELATIONSHIPS OF *SISICOTTUS HIBERNUS* (ARANEAE, LINYPHIIDAE, ERIGONINAE)

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ABSTRACT. *Carorita hiberna* NEW COMBINATION, a species with many putative autapomorphies known from one sex and few specimens, is transferred from *Sisicottus*. This transfer is based on a modified version of a cladistic analysis of erigonine relationships by G. Hormiga which incorporated 43 spider taxa scored for 73 characters. The modified analysis features 46 taxa scored for 74 characters. The resulting cladogram placed *C. hiberna* sister to *C. limnaea*, the type species of *Carorita*. It is concluded that *C. hiberna* is better placed in *Carorita* than in either a new monotypic genus or in *Sisicottus*. *Carorita hiberna* is redescribed and the monophyly of *Carorita* as currently circumscribed is discussed.

Carorita hiberna (Barrows 1945) NEW COMBINATION (Linyphiidae, Erigoninae) was inexplicably described as a member of the genus *Sisicottus* Bishop & Crosby 1938. *Carorita hiberna* is a very unusual erigonine species that shares none of the synapomorphies that unite *Sisicottus* (Zujko-Miller 1999). *Carorita hiberna* is known only from three male specimens from the Great Smoky Mountains National Park, North Carolina, USA. After revising *Sisicottus* (Zujko-Miller 1999), I was left with three alternatives as to the fate of *C. hiberna*: I could keep it in *Sisicottus*, which would leave *Sisicottus* polyphyletic; I could erect a new monotypic genus for it; or I could transfer it to the genus which contains its closest relatives. *Carorita hiberna* features many apparently apomorphic character states in the form of the male palpus, and it was not obvious to me what genus contained its closest relatives. I chose to seek the closest relatives of *C. hiberna* using phylogenetic methods. By placing *C. hiberna* in a phylogenetic context, I was able to formulate a testable phylogenetic hypothesis. My cladistic analysis identified *Carorita limnaea* (Crosby & Bishop 1927), the type species of *Carorita* Duffey & Merrett 1963, as the sister taxon of *C. hiberna*. With the transfer of *C. hibernus*, *Carorita* currently contains three species.

METHODS

I cleared specimens in methyl salicylate (Holm 1979) and positioned them for illustration using a temporary slide mount (Coddington 1983). I made sketches using a camera lucida fitted to a Leica DMRM compound microscope at 400×. Further observations were made using a Leica MZ APO dissecting microscope. Museum acronyms for specimen depositories appear in the acknowledgments.

CLADISTIC ANALYSIS

The cladistic analysis by Hormiga (in press) is the most rigorous hypothesis of erigonine relationships to date and is the logical starting point for questions of relationships within the Erigoninae. The original analysis incorporates 43 terminal taxa, including 31 erigonine genera, scored for 73 characters. My modified version of Hormiga's analysis incorporates three additional taxa, one new character, and one recoded character.

Carorita hiberna, *C. limnaea*, and *Sisicottus montanus* (Emerton 1882) were added to Hormiga's (in press) matrix. *Carorita limnaea* was included because it appears to share some potentially synapomorphic character states with *C. hiberna* including a looped sperm duct in the tegulum, a tuberculate radical tailpiece, and a suprategulum separated from the tegulum by a membranous region so that it appears to form a distinct sclerite. *Sisicottus* was included to test the implicit phylogenetic hypothesis of Barrows (1945) that *C. hiberna* plus *Sisicottus* form a monophyletic group.

Several character states remain unknown for *C. hiberna* because females are unknown and males are rare and not available for irreversible methods of examination. The male cephalothorax was not examined using scanning electron microscopy to search for cuticular pores in the clypeal region (character 50) or to examine details of the stridulatory striae on the chelicerae (character 56). No abdomens were digested for examination of the tracheal system (characters 51, 52). *Carorita hiberna* was coded as follows: 0001310110 1210110101 1201000101 3????????? 000000000? ??001?0??1 00011?0??1 1??1

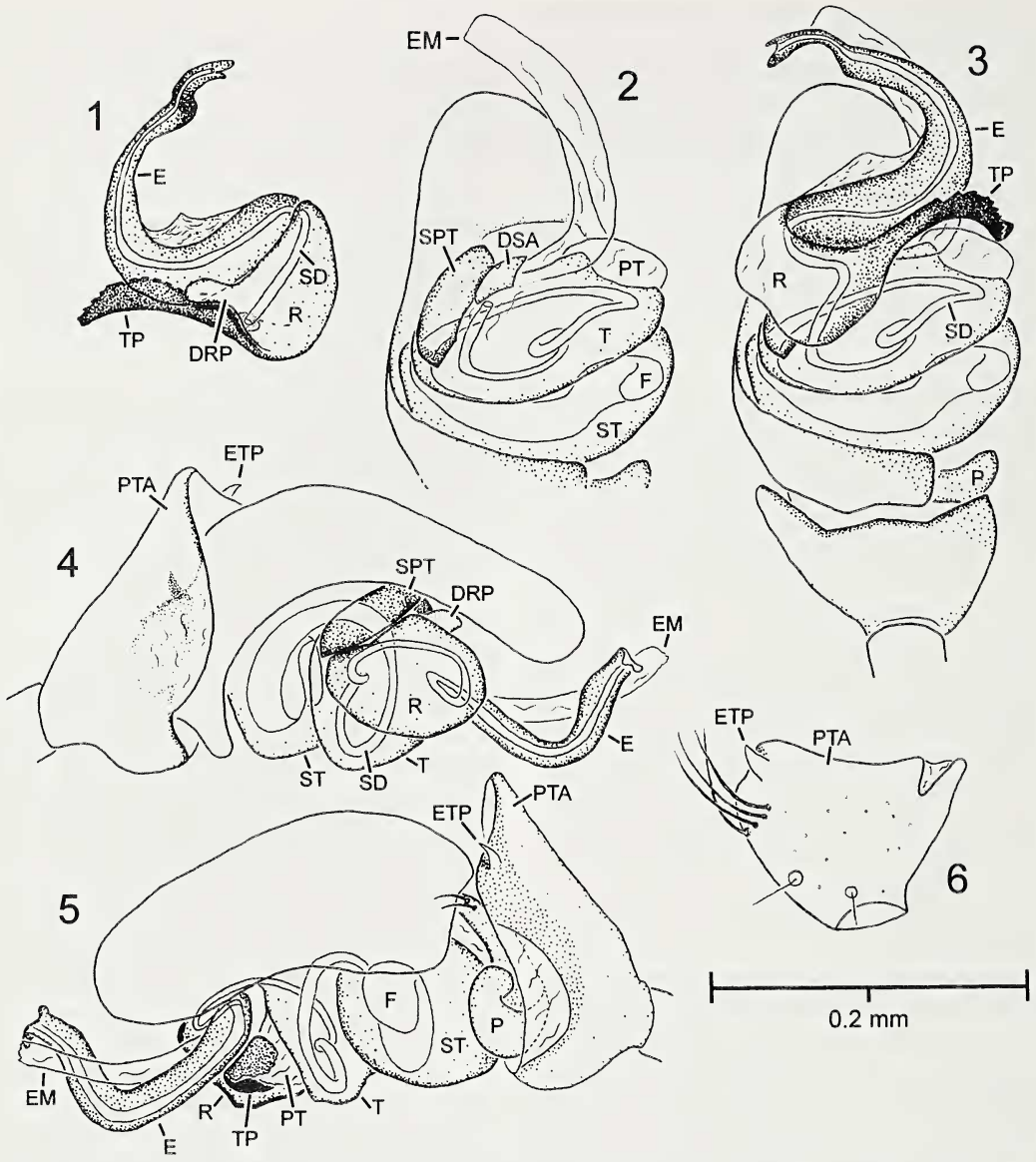
Carorita limnaea was coded as follows: 0001310110 1210110101 1501000101 300–000100 0000000000 0–00120111 0011100101 1??1. *Carorita limnaea* was given a unique character state for the shape of the radical tail piece (character 22). In *C. limnaea*, the tailpiece extends both dorsally and ventrally from its origin distal to the origin of the embolus. Coding of *C. limnaea* was based on examination of the following specimens: **UNITED STATES:** *Maine:* Piscataquis County, 2.3 km ESE of Soubunge Mtn., dense spruce-fir forest, Line I, Stn, 1, T4 R11, WELS, 1 June 1978, pitfall collection, 1♂, (D.T. Jennings, M.W. Houseweart, USNM); *New York:* McLean, mud pond, 42°32′N, 76°18′W, 30 May 1921, 8♂17♀, (C.R. Crosby, AMNH).

Sisicottus montanus was coded as in Zujko-Miller (1999). Character 74 was scored with a zero. Coding of *S. montanus* was based on examination of the following specimens: **UNITED STATES:** *Massachusetts:* Berkshire County, Mt. Greylock, 3400 feet, deciduous litter, 15 October 1990, 2♂1♀, (R.L. Edwards, USNM).

Hormiga's (in press) analysis was modified by the addition of one new character and the recoding of an existing character. Both characters pertain to structures that are synapomorphies of the Linyphiidae (the suprategulum and the linyphiid radix) so character states for linyphiid taxa other than *C. limnaea*, *C. hiberna*, and *S. montanus* were determined using Hormiga (1994, in press). Character 74 is the texture of the radical tailpiece which is tuberculate in *C. limnaea* and *C. hiberna*. In all other taxa with a radical tailpiece, this sclerite is more or less smooth. Taxa without a radical tailpiece were coded as inapplicable for this character. The junction between the tegulum and the suprategulum (character 12) was recoded. Character 12 documents the membranous hinge between the tegulum and the suprategulum in *Stemonyphantes* Menge 1886 (van Helsdingen 1968; Hormiga 1994). In the context of Hormiga's analysis, this character state is autapomorphic and character 12 is not phylogenetically informative. I have added a third state to character 12 and it is now coded as follows: Suprategulum: 0 = continuous with tegulum; 1 = articulated; 2 = separate from tegulum (Figs. 7, 9). In *Carorita limnaea*, *C. hiberna*, *Asthenargus paganus* (Simon 1884), *Gongyliellum vivum* (O. Pickard-Cambridge 1875) and *Erigone psychrophila* Thorell 1871, there is a membranous division between the sclerotized parts of the tegulum and the suprategulum so that the suprategulum appears to be a distinct sclerite rather than a more heavily sclerotized distal portion of the tegulum. This is the new character state coded as 2. In most other linyphiids, the tegulum and the suprategulum are joined by a region of continuous sclerotization and only part of the junction between the tegulum and the suprategulum is membranous. In *Stemonyphantes*, the junction between the tegulum and the suprategulum is a wide flexible hinge (Hormiga 1994, fig. 2c). Also, the tegular-suprategular junction is unusual in *Stemonyphantes* because it is on the ventral face rather than the mesal face of the palpal bulb.

Analysis.—I used PAUP version 3.1 (Swofford 1993), Hennig86 version 1.5 (Farris 1988) and NONA version 1.6 (Goloboff 1993) to search the data (46 taxa, 74 characters) for the most parsimonious topology. In PAUP, I ran a heuristic search with 100 replicates of random taxon addition subjected to tree bisection-reconnection branch swapping. In Hennig86, I used the "mh*,bb*" search strategy. In NONA, I ran a search under the "amb=" setting (modified rule 3; see Coddington & Scharff 1994; Zujko-Miller 1999) with the "mult*" random taxon addition algorithm for 100 replicates followed by the "max*" branch-swapping algorithm. I used MacClade (Maddison & Maddison 1992) to analyze character optimization.

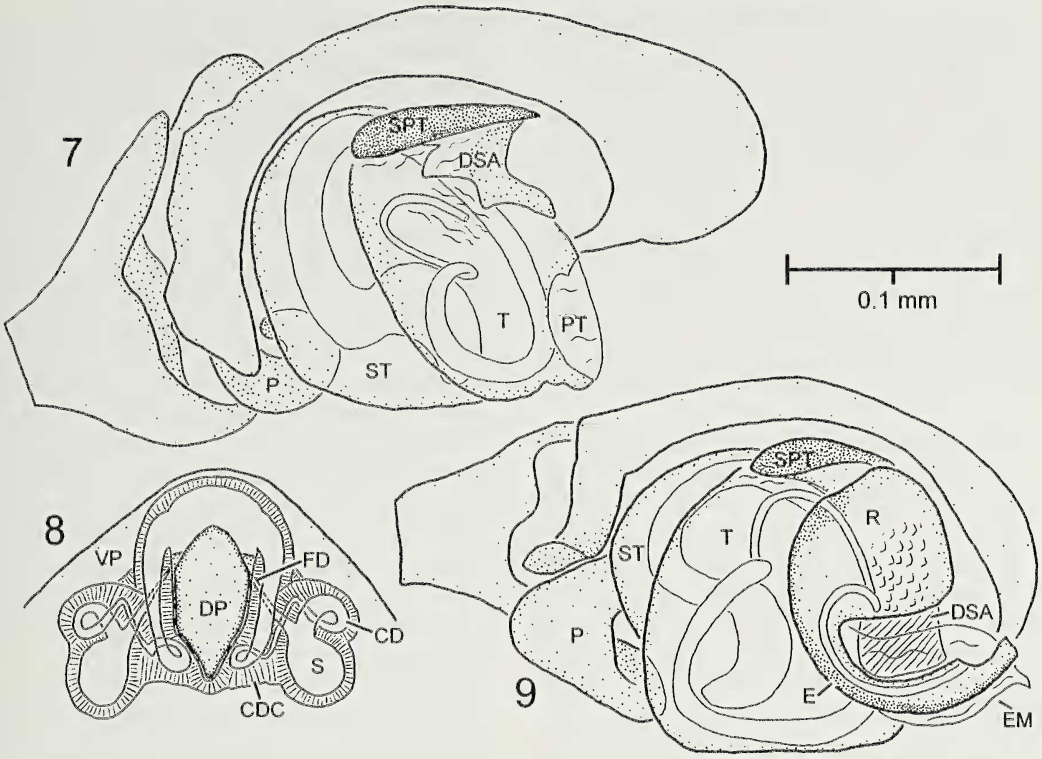
Successive character weighting (Farris 1969; Carpenter 1988) by the maximum value of the rescaled consistency index was performed in PAUP with the base weight set to



Figures 1–6.—Palpus of male *Carorita hiberna* from Thomas Ridge, North Carolina. 1. Embolic division, dorsal view; 2. Ventral view with embolic division removed; 3. Ventral view; 4. Mesal view; 5. Ectal view; 6. Palpal tibia, dorsal view. *Abbreviations:* DRP, dorsal radical process; DSA, distal suprategular apophysis; E, embolus; EM, embolic membrane; ETP, ectal tibial process; F, fundus; P, paracymbium; PT, protegulum; PTA, palpal tibial apophysis; R, radix; SD, sperm duct; SPT, suprategulum; ST, subtegulum; T, tegulum; TP, radical tail piece.

1000. Trees found by Hennig86 and NONA were imported into PAUP. NONA trees were saved using the "ksv*" command. PAUP will arbitrarily resolve polytomies in trees saved using the "sv" command in NONA. The solution set from all three programs (PAUP, Hennig86, and NONA) was combined. Duplicate trees were eliminated. The remaining unique trees were then filtered to exclude polytomous trees when more highly resolved compatible trees were found (Coddington & Scharff 1996). This set of trees was re-weighted and the data re-analyzed in PAUP.

Results.—PAUP, Hennig86, and NONA and all found multiple trees of 236 steps (calculated after excluding uninformative charac-



Figures 7–9.—Genitalia of *Carorita* species. 7. Male palpus of *C. hiberna* from Thomas Ridge, North Carolina, mesoventral view with embolic division removed; 8, 9. *Carorita limnaea* from McLean New York; 8. Cleared epigynum, ventral view; 9. Male palpus, ventromesal view. *Abbreviations:* CD, copulatory duct; CDC, copulatory duct capsule; DP, dorsal plate of epigynum; DSA, distal suprategular apophysis; E, embolus; EM, embolic membrane; FD, fertilization duct; P, paracymbium; PT, protegulum; R, radix; S, spermatheca; SPT, suprategulum; ST, subtegulum; T, tegulum; TP, radical tail piece; VP, ventral plate of epigynum.

ters) with a consistency index (CI) of 0.377 and a retention index (RI) of 0.673. PAUP found 63 trees, Hennig86 found 33 trees, and NONA found 45 trees. A total of 78 unique most parsimonious trees were found. Of these, 24 trees were more highly resolved but otherwise compatible with other most parsimonious trees. All trees place *Carorita limnaea* sister to *Carorita hiberna*. A strict consensus of all most parsimonious trees has a trichotomy composed of the *Carorita* clade, *Asthenargus paganus* and *Gongylidiellum vivum*. This clade is part of an 11-tomy composed of various erigonine terminals and clades. Successive character weighting stabilizes on six trees. All six trees are 236 steps long under equal weights and were among the original set of 78 trees. Except for the additional taxa, this set of six trees is identical to the result found in Hormiga's (in press) original analysis. Disagreement among the six trees is found in two places: the relationships among the linyphiines, micronetines and all other linyphiids and the relationships among *Drepanotylus* Holm 1945, *Sciastes* Bishop & Crosby 1938 and the "distal erigonines" clade. The "distal erigonines" clade is fully resolved and identical in all six trees. The "distal erigoinines" clade features a monophyletic *Carorita* clade sister to *Gongylidiellum vivum*. *Sisicottus* remains in the position reported by Zujko-Miller (1999), sister to *Oedothorax gibosus* (Blackwall 1841).

Implications.—The two species which formerly composed *Carorita* have traditionally been united based on their chaetotaxy (especially the presence of a prolateral macroseta on tibia I), the large paracymbium, the form of the suprategular apophysis, overall palpal conformation, the general form of the palpal

tibia, the relatively long tarsi, and proportional characteristics of the eyes (Duffey 1971; Millidge 1977). Millidge (1977) considered *C. limnaea* and *C. paludosa* Duffey 1971 to be members of a monophyletic group despite conspicuous differences in the form of the embolic division and cited it as evidence of how greatly the embolic division can vary within an otherwise "good" genus. Unfortunately, I have been unable to test this claim since I have not been able to examine specimens of *C. paludosa* and existing descriptions and illustrations are not adequate for scoring many of the characters in the matrix.

Optimization.—This analysis indicates that the genus *Carorita* can be defined phylogenetically on the basis of two unambiguous synapomorphies: the presence of a radical tailpiece (character 21) and the loss of a lamella characteristica (character 27). Although *C. paludosa* has a large mesal sclerite of the embolic division (Millidge 1977, fig. 159), I have been unable to determine from published descriptions whether it is a radical tailpiece or a lamella characteristica. Five characters can be optimized to provide additional support for the monophyly of *Carorita*. However, these five characters could also be placed on alternative tree nodes without affecting tree length. These are the presence of papillae on the protegulum (character 9; unknown in *C. paludosa*), a long embolus (character 17; short in *C. paludosa*), the shape of the radical tailpiece (character 22; unknown in *C. paludosa*), encapsulation of the epigynum (character 38; unknown in *C. hiberna* and *C. paludosa*), and a tuberculate radical tailpiece (character 74; unknown in *C. paludosa*). Although *C. limnaea* and *C. hiberna* are the only taxa in the analysis with a tuberculate radical tailpiece, their two closest relatives, *Asthenargus paganus*, and *Gongylidiellum vivum*, both lack a radical tailpiece and were therefore coded as inapplicable for this character. A generic revision of *Carorita* with a strong phylogenetic component should be undertaken in the near future to address the placement of *C. paludosa*.

All three *Carorita* species feature a strong kink or loop in the path of the sperm duct in the tegulum near the junction between the tegulum and the suprategulum (Figs. 7, 9; Millidge 1977, fig. 159). Most other erigonines have a sperm duct that follows a smooth curve through the tegulum. However, when I attempted to code this as a cladistic character, I found a spectrum of conditions rather than a small number of discrete character states. Nevertheless, the presence of a kink in the sperm duct is a useful part of the diagnosis of *Carorita*.

Missing data.—Attributes of the tracheal system have long been relied upon as characters in linyphiid classification (Blest 1976; Millidge 1984, 1986). Hormiga (in press) demonstrated that these characters have high consistency. This analysis optimizes *C. hiberna* as having the haplotracheate condition, although no observation of the tracheal system of *C. hiberna* has been made. If *C. hiberna* is speculatively coded as having the desmitracheate condition (1: character 51) with no taenidia (0: character 52), 328 unique most parsimonious trees of 237 steps result (192 trees in Hennig86, 246 trees each in NONA and PAUP; CI = 0.376, RI = 0.670).

A total of 102 of these trees are more resolved than otherwise compatible trees. The strict consensus of these 102 trees has little phylogenetic structure. It features a polytomy of 21 clades and individual taxa at the node which represents the Erigoninae. *Carorita limnaea* and *C. hiberna* are not consistently monophyletic and form two of the branches in this 21-tomy. Successive character weighting of these 102 trees stabilizes on 30 trees (CI = 0.372, RI = 0.666). These trees are two steps longer under equal weights than the most parsimonious trees. The strict consensus of these 30 trees forms a topology unlike that found by Hormiga (1999), especially in the deep nodes. *Carorita limnaea* and *C. hiberna* form a paraphyletic assemblage rather than a monophyletic group. Under the assumption that *C. hiberna* is haplotracheate rather than desmitracheate without taenidia, the data are found to be more internally consistent and the resulting phylogenetic hypothesis that is consistent with the previous hypothesis (Hormiga in press), one which suffered from few missing observations.

DISCUSSION

Phylogenetic hypotheses can be communicated either implicitly as higher taxonomic names or explicitly in the form of a cladogram. If taxonomy is to reflect phylogenetic history, genera should serve as implicit hy-

pothesis that a particular group of species share a unique common ancestor. However, monotypic genera do not provide this grouping information and thus cannot be considered phylogenetic hypotheses. On the other hand, cladistic analyses by their nature explicitly convey detailed phylogenetic hypotheses. The ranks and labels assigned to nodes in a cladogram are less critical since the hypothesis of relationships is fully expressed in the tree. As part of an explicit phylogenetic hypothesis, detailed grouping information is available and monotypic genera are less problematic.

The placement of *Carorita hiberna* was difficult because of the many apparently autapomorphic character states exhibited by this species. However, no matter how many autapomorphic character states are found in a particular species, it must still have a sister taxon (Platnick 1976). Placing *Carorita hiberna* in a new monotypic genus without identifying its putative sister taxon would have been an abdication; a lack of a grouping hypothesis. As it stands, my circumscription of *Carorita* is based on explicit evidence and is subject to falsification given sufficient new evidence. Although these conclusions reflect the best available evidence, missing data has led to the optimization of some character states based on inference (Platnick et al. 1991). When additional specimens are discovered, the predictions of this analysis should be tested.

Between 1981 and 1995, over 70% of new linyphiid genera have been monotypic (Platnick 1989, 1993, 1997). The volume of new monotypic genera generated within the Linyphiidae indicates a critical lack of phylogenetic consideration. A phylogenetic approach based on morphological characters demands careful examination of comparative anatomy but the result is a rich hypothesis not only of taxonomic relationships but of character evolution. A broad phylogenetic context will be very helpful for associating monotypic genera with their relatives. This will no doubt lead to the synonymization of many existing genera. Ultimately, the utility of the linyphiid taxonomic system will be greatly improved. However, I have attempted to demonstrate that we do not need to wait for some grand phylogenetic hypothesis of the Linyphiidae. The basic context for applying phylogenetic criteria to new work in linyphiid systematics is already available.

TAXONOMY

Carorita Duffey & Merrett 1963

Carorita Duffey & Merrett 1963:573–576, figs. 1–8 (♂,♀). Duffey 1971: 14–15, figs. 1–8 (♂,♀). C Locket, Millidge & Merrett 1974: 92–94, figs. 56a-g (♂,♀). Blest 1976: 188. Millidge 1977: 40, figs. 158, 159 (♂); 1984: 245–246. Brignoli 1983: 328. Roberts 1987: 108, figs. 53d, 53e (♂,♀). Platnick 1989: 223; 1993: 252; 1997: 328. Heimer & Nentwig 1991: 124, figs. 352.1–353.4 (♂,♀). Type species by original designation and by monotypy, *Oedothorax limnaeus* Crosby & Bishop 1927: 149–150, figs. 11–14.

Diagnosis.—Males of *Carorita* can be distinguished from most other erigonines by the form of the suprategulum which has a distinct boundary at its origin and by the kinked or looped path of the sperm duct through the tegulum (Figs. 7, 9). They are distinguished from males of other erigonines with these character states by the absence of a lamella characteristica and the presence of a radical tail piece (uncertain in *C. paludosa*). Females can be distinguished from other erigonines by the complex, anteriorly-projecting looped path of the copulatory ducts (Fig. 8).

Description.—Tibial macrosetae 2-2-1-1 (except in *C. hiberna*: 2-2-2-1); Tm IV absent. Tibia I with one distal prolateral macroseta (absent in *C. hiberna*). At least in *C. limnaea*, chelicerae with imbricated stridulatory files and median tracheal trunks unbranched, shorter than laterals, confined to abdomen (Blest 1976; haplotracheate *sensu* Millidge 1984). *Males:* Palpal tibia with one prolateral and one retrolateral trichobothrium. *Carorita limnaea* and *C. hiberna* (but not *C. paludosa*) with long embolus in frontal plane, radix with tuberculate tailpiece and no anterior radical process (Figs. 3, 9). Distal part of cymbium and ectal side of palpal tibia with clusters of macrosetae. *Females:* Females of *C. paludosa* have not been examined and details of female genitalia cannot be unambiguously interpreted using published descriptions and illustrations; females of *C. hiberna* unknown; females of *C. limnaea* with posteriorly oriented ventral plate invagination leading to copulatory openings; copulatory ducts encapsulated with loop at anterior maximum and again posterior to spermathecae near junction. Fertilization ducts project posteriomesally from spermathecae (Fig. 8).

Composition.—*Three species: Carorita limnaea* (Crosby & Bishop 1927), *C. paludosa* Duffey 1971 and *C. hiberna* (Barrows 1945).

Distribution.—North America (*C. limnaea*, *C. hiberna*) and Europe (*C. limnaea*, *C. paludosa*).

Carorita hiberna (Barrows 1945)
NEW COMBINATION
Figs. 1–7

Sisicottus hibernus Barrows 1945: 74, figs. 1, 2 (♂). Brignoli 1983: 356.

Type.—Male holotype from United States: North Carolina, Great Smoky Mountains National Park, Mingus Creek, 1 February 1943, in OSU, examined.

Diagnosis.—Males of *C. hiberna* are readily distinguished from other *Carorita* species by the unusual, complex shape of the embolus which runs in a more or less frontal plane (Fig. 3E), by their long, ectally projecting, tuberculate, radical tailpiece (Fig. 3TP), by the horn-like process on the ectal side of the palpal tibia (Fig. 6ETP), by the presence of a distal macroseta on tibia III, by the absence of a prolateral macroseta on tibia I, and by the presence of a dorsal radical process (Fig. 1, DRP).

Description.—*Male:* (from Thomas Ridge, North Carolina). Carapace length = 0.6 mm. Tibial macrosetae weak; 2-2-2-1; Tm I = 0.34. Chelicerae with 5–6 promarginal teeth; 5 retromarginal teeth with proximal 2 larger than distal 3. Embolus describing a semicircular arc in more or less frontal plane with outside of curve ectal; tip of embolus arced in nearly transverse plane with outside of curve dorsal (Figs. 1, 3E). Embolic membrane long, narrow, curved with outside ectal (Fig. 2EM). Radix with anteriomesally projecting tuberculate tailpiece (Fig. 3TP) and ectodorsally projecting dorsal radical process (Fig. 1DRP). Protegulum on ectal side of bulb (Fig. 2PT). Palpal tibia with long, straight apophysis with flat distal margin; horn-like process on ectal side of apophysis; ectal and mesal sides of palpal tibia both with regions of semitransparent chitin (Figs. 4-6). *Female:* Unknown.

Distribution.—Known only from the Great Smoky Mountains National Park, North Carolina.

Material examined.—UNITED STATES: *North Carolina:* Swain County, Great Smoky Mountains National Park, Mingus Creek, 1 February 1943, 1♂, (holotype, Barrows, OSU); Swain County, Great Smoky Mountains National Park, Thomas Ridge, ca. 200 m from trailhead at route 441, west-facing slope below trail, 4540 feet, old growth mixed hardwood, UTM: E3107, N39436, 22 September 1994, 1 m^2 litter sample, 1♂, (Cribbs team, GSMNP); Haywood County, Great Smoky Mountains National Park, Cataloochee, 150 m south of mouth of Palmer Branch at Caldwell Fork, 2800–3000 feet, old growth hemlock, UTM: E3107, N39436, 23–31 March 1997, pitfall trap, 1♂, (Coyle, Edwards & Wright, GSMNP) North Carolina, Great Smoky Mountains National Park.

Natural history.—*Carorita hiberna* is known only from three male specimens collected in the Great Smoky Mountains National Park. The rarity of this species in the face of intensive collecting efforts by Dr. Frederick Coyle (Western Carolina University) and his collaborators within the park raise questions about the long term prospects for the continued survival of this species. The rare diplurid spider *Microhexura montivaga* Bishop & Crosby 1925 is known only from spruce and Fraser fir forests in the southern Appalachians and is currently listed as a federally protected endangered species (Coyle 1981; Fridell 1995). The staphylinid beetle *Dasycerus bicolor* Wheeler & McHugh 1994 and the linyphiid spider *Sisicottus montigenus* Bishop & Crosby 1938 are both endemic to this same region and habitat type, have experienced recent and dramatic declines in their populations, and may be worthy of similar protected status (Wheeler & McHugh 1994; Zujko-Miller 1999). However, *C. hiberna* has been found in both mixed hardwood and hemlock forests. It does not appear to be associated with the declining spruce-fir habitat and though rare, there is no evidence that its population has actually declined since its discovery.

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